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Local Feedback Signals Are Not Distorted By Prior Eye Movements: Evidence From Visually Evoked Double Saccades

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Goossens, H.H.L.M. and A. J. Van Opstal. Local feedback signals are not distorted by prior eye movements: evidence from visually evoked double saccades. *J. Neurophysiol.* 78: 533–538, 1997. Recent experiments have shown that the amplitude and direction of saccades evoked by microstimulation of the monkey superior colliculus depend systematically on the amplitude and direction of preceding visually guided saccades as well as on the postsaccade stimulation interval. The data are consistent with the hypothesis that an eye displacement integrator in the local feedback loop of the saccadic burst generator is gradually reset with a time constant of ~ 45 ms. If this is true, similar effects should occur during naturally evoked saccade sequences, causing systematic interval-dependent errors. To test this prediction in humans, saccades toward visual single- and double-step stimuli were elicited, and the properties of the second saccades were investigated as a function of the intersaccadic interval (ISI). In 15–20% of the saccadic responses, ISIs fell well below 100 ms. The errors of the second saccades were not systematically affected by the preceding primary saccade, irrespective of the ISI. Only a slight increase in the end-point variability of second saccades was observed for the shortest ISIs. These results are at odds with the hypothesis that the putative eye displacement integrator has a reset time constant > 10 ms. Instead, it is concluded that the signals involved in the internal feedback control of the saccadic burst generator reflect eye position and/or eye displacement accurately, irrespective of preceding eye movements.

INTRODUCTION

It is commonly assumed that saccadic eye movements are driven by a neural feedback circuit in which a desired eye movement is compared with an internal representation (efference copy) of the actual movement. In this way it can be readily understood that saccades remain accurate, in the absence of visual feedback, despite considerable variability in their kinematics (Jürgens et al. 1981). Controversy exists, however, on the nature of the involved signals.

In the classical model of the saccadic burst generator (Robinson 1975) (see Fig. 1A), desired eye position (DP) is compared with an internal feedback signal that represents current eye position (efference copy, EP). This comparison yields a dynamic motor error signal (ME; $ME = DP - EP$) that drives the burst generator until the eyes reach the desired end position ($ME = 0$). Current eye position is derived from the eye position integrator (NI) by temporal integration of eye velocity (\dot{E}). The latter is produced by the brain stem saccadic burst generator.

More recent displacement models (Jürgens et al. 1981; Scudder 1988) (see Fig. 1B), however, assume that a desired eye displacement signal, presumably emanating from the superior colliculus (SC), drives the hypothesized feed-

back loop. In these models, dynamic motor error is obtained by comparing this desired eye displacement (DD) with an efference copy of the actual eye displacement (ED; $ME = DD - ED$). The latter signal is generated by a displacement integrator (DI). This so-called resettable integrator integrates eye velocity, just like the position integrator, but needs to be reset to zero after each saccade.

So far, it has been difficult to experimentally dissociate the two classes of models. Recently, however, Nichols and Sparks (1995) noted that the existence of a neural DI in the feedback pathway may be revealed if it resets gradually, rather than instantaneously (Jürgens et al. 1981). In that case, it is predicted that saccades are influenced by preceding eye movements when there is insufficient time for a complete reset. Depending on its initial state, the DI would produce an erroneous feedback signal of current eye displacement, causing a mismatch between desired and actual eye displacement. If so, systematic changes in the resulting saccade metrics as a function of the intersaccadic interval (ISI) are expected.

Indeed, when the monkey SC was electrically stimulated immediately after a visually evoked saccade, the vector of the induced eye movements systematically deviated from the fixed-vector control saccade (Kustov and Robinson 1995; Nichols and Sparks 1995). This behavior was consistent with the predictions of the displacement model, assuming a gradual resetting DI in the feedback loop (reset time constant ~ 45 ms). It was argued that these findings refute Robinson's model, which predicts no time-dependent interactions between two successive saccades.

If the observed effects on saccades are truly caused by a gradual resetting DI, similar effects should be expected when subjects make naturally evoked sequential eye movements. After all, the DI is assumed to be part of the local feedback loop that controls the execution of saccadic eye movements, irrespective of how they are evoked.

To our knowledge, there are no reports in the oculomotor literature that indeed describe such time-dependent behavior under natural conditions. In fact, observations by Becker and Jürgens (1979) (human subjects) suggest that the second saccade in a visual double-step paradigm remains quite accurate, even when the ISI is very short. However, these data were not presented in a quantitative form, making it difficult to infer to what extent the results contrast with the aforementioned neurophysiological data. We therefore decided to investigate oculomotor performance of human subjects during short-interval saccade sequences in more detail.

To that end, visual double-step stimuli were presented that frequently evoked two saccades in rapid succession.

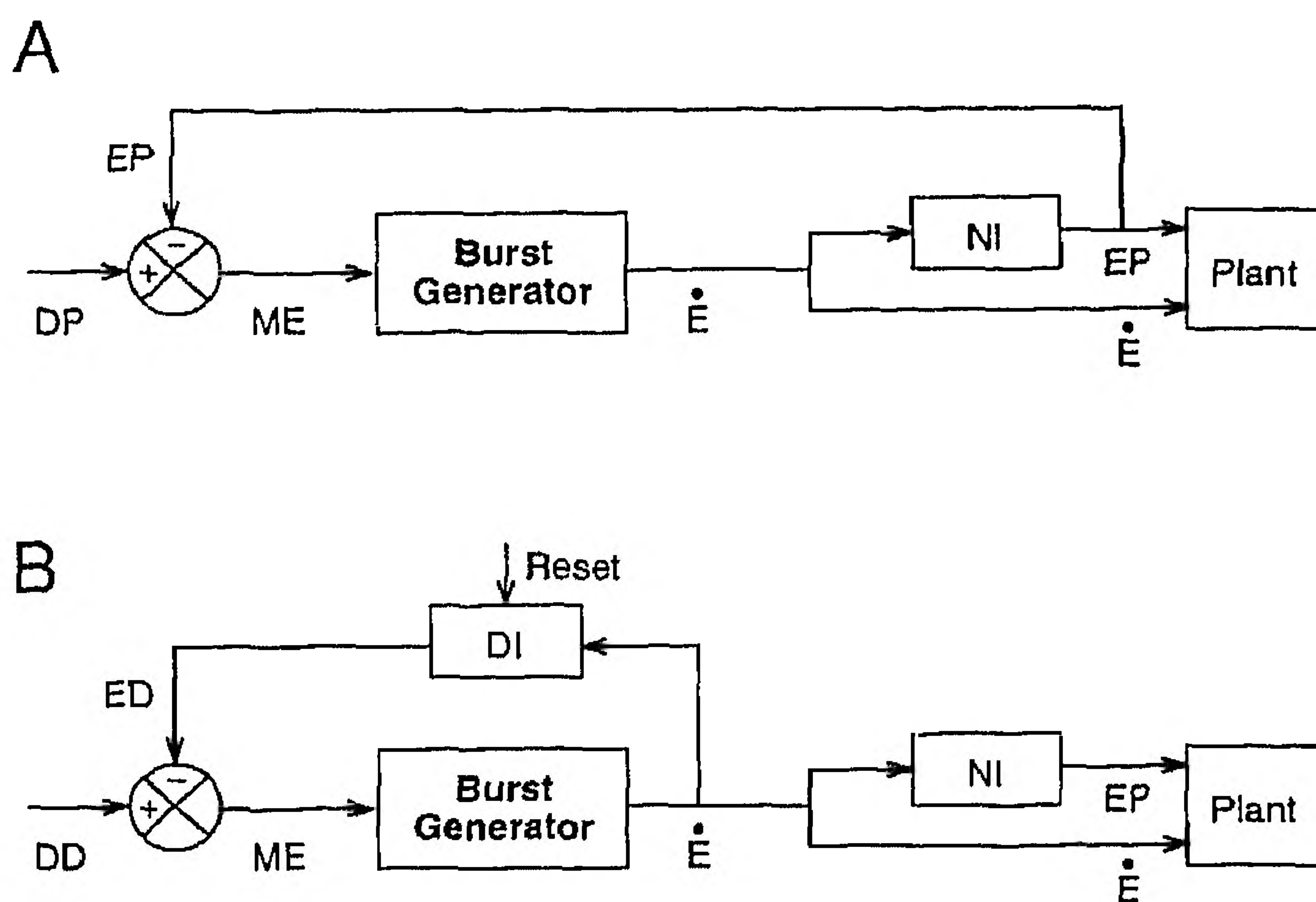


FIG. 1. A: simplified diagram of eye position feedback model (Robinson 1975). B: displacement feedback model adapted from Jürgens et al. (1981). NI, eye position integrator; DI, eye displacement integrator (with reset signal); DP, desired eye position (in reference to head); DD, desired eye displacement; EP, current eye position (efference copy); ED, current eye displacement (efference copy); ME, dynamic motor error; \dot{E} , eye velocity.

Saccades were also elicited by single, visual targets, randomly presented in the visuomotor field. A peculiar consequence of the “gradual reset” hypothesis is that correction saccades, often occurring in the latter paradigm, would not be corrective when made briefly after the primary saccade.

The aim of the present experiments was to test the properties of the local feedback circuit rather than the programming of double-step saccades. Our goal thus contrasts with the seminal double-step experiments by Hallett and Lightstone (1976) and Mays and Sparks (1980). Those experiments indicated that both retinal and extraretinal signals are used to make accurate saccades. How these signals are combined, and which extraretinal signals are involved (eye position or eye displacement), is still a matter of debate (see, e.g., Goldberg and Bruce 1990; Schlag et al. 1994). Nevertheless, if there is indeed a time-dependent flaw in the control of the burst generator, as proposed by the gradual reset hypothesis, it is expected that any saccade triggered briefly after a preceding saccade will be affected, regardless of how it was prepared.

Note, however, that motor performance is quantified by measuring saccade accuracy (see METHODS). It was therefore necessary to assure that subjects could localize the targets very well. After all, if systematic errors are indeed encountered, they should result from properties of the proposed eye DI, rather than from mechanisms involved in saccade preparation. For this reason, subjects were tested with stimuli in which the (final) target remained present throughout the entire response.

METHODS

Setup

Subjects (head fixed) faced a spherical array of light-emitting diodes (radius 85 cm) in an otherwise completely dark room. Two-dimensional search coil signals were amplified, filtered (low-pass, 150 Hz), and sampled at 500 Hz per channel.

Subjects

All subjects ($n = 5$) were accustomed to wearing search coils and were informed about the purpose of this investigation.

Double-step paradigm

According to the gradual reset hypothesis, the largest effects on saccade metrics are obtained at 1) the shortest ISIs in combination with 2) large primary saccades (see Eq. 1 below). To elicit large primary saccades, an eccentric fixation spot (F) was initially presented for a random period of 800–1,600 ms at 35° to the left of the center. Subsequently, two targets (T1 and T2) were presented in rapid succession on the horizontal meridian. Subjects were required to follow both targets as fast as possible.

Two different stimulus configurations were randomly offered in each session. The applied configurations (F|T1|T2) were either 1) $-35|0|+9^\circ$ and $-35|+5|+14^\circ$ (i.e., 2nd target jump $\Delta T = 9^\circ$) or 2) $-35|0|+14^\circ$ and $-35|+5|+20^\circ$ ($\Delta T \approx 14^\circ$). In this way, a large number ($N > 300$) of comparable responses could be elicited within a single recording session of ~ 35 min.

To reduce saccade latencies, a gap was included between F offset and T1 onset (50–100 ms) and between T1 offset and T2 onset (50–80 ms). T1 was flashed for 10–40 ms, whereas T2 remained visible for 600 ms. The intensity of the stimuli was 0.20 cd/m^2 .

The precise timing of the stimulus events was adjusted to each subject's behavior. This was necessary, first, to ensure that T2 was present before the primary saccade started (by 50–200 ms), and second, to minimize saccade averaging effects (Becker and Jürgens 1979; Ottes et al. 1984). Note that T2 was still visible at the end of the second saccade. In this way, the saccadic system could use all possible information to prepare the second saccade toward T2 as accurately as possible (see INTRODUCTION).

To probe for the occurrence of predictive responses, a small number (10%) of single-step catch trials was randomly interleaved with the double-step stimuli. In these catch trials, only one peripheral target was presented at either the location of T1 or T2.

To be able to compare the accuracy of the saccades in the double-step sequence with saccades to single targets presented in isolation, single-target control stimuli were presented in a separate block of trials. This block consisted of target steps from F to T1, F to T2, and T1 to T2, respectively.

Single-step paradigm

Subjects were asked to make saccades from the straight-ahead fixation spot to a randomly selected peripheral target that was visible for 900 ms. Targets were presented at polar coordinates $R \in [2, 5, 9, 14, 20, 27, 35]^\circ$, and $\Phi \in [0, 30, 60, 330]^\circ$. Thus the total set consisted of 84 different stimulus configurations.

Data analysis

Saccades were detected off-line with a computer algorithm that used separate velocity and mean acceleration criteria for saccade onsets and offsets. All saccade markings were visually inspected and corrected, if necessary.

The initial and final eye positions were determined for each saccade vector. From these, the horizontal and vertical eye displacement components were calculated. For each second saccade, the difference between its end position and final target location (saccade error) was computed, as well as the difference between initial eye position and final target location (initial motor error). This procedure was performed separately for horizontal and vertical eye movement components. The ISI was defined as the time difference between the offset of the first saccade and onset of the second saccade.

If the DI is reset gradually, it is predicted that the horizontal/vertical error remaining after the second saccade is a function of the horizontal/vertical displacement component of the primary saccade vector and the ISI according to (Kustov and Robinson 1995; Nichols and Sparks 1995)

$$E2 = -S1 \cdot \exp(-ISI/\tau) \quad (1)$$

where $E2$ is the saccade error ($E2 < 0$: saccade ends leftward/downward from the target), $S1$ is the displacement component of the primary saccade vector (right/up positive, left/down negative), and τ (ms) is the reset time constant of the putative DI. In the model predictions, presented below, the value of the time constant was fixed at $\tau = 40$ ms, which is on the low end of the values determined in the SC stimulation experiments.

RESULTS

Figure 2 displays a number of superimposed double-step responses aligned with the offset of the primary saccade. If the execution of saccades is indeed influenced by preceding eye movements (see INTRODUCTION), systematic, interval-dependent errors should occur in the second saccades. In our double-step paradigm, these saccades should become increasingly hypometric at short ISIs, and even reverse in direction at very short ISIs (i.e., ~ 50 ms or less, see Eq. 1).

Note, however, that the second saccade always ends near the second target, $T2$, even though the ISIs are short ($40 < ISI < 150$ ms), and the preceding eye movements are large ($34 < S1 < 42^\circ$). Reversals in saccade direction were never observed in double-step trials. Also notice the systematic overshoots (in reference to $T1$) of the primary saccades, which is presumably due to saccade averaging (Becker and Jürgens 1979; Ottes et al. 1984).

Figure 3 depicts the results of a double-step experiment for two of our subjects. *A* and *B* show the distributions of the observed ISIs. Note, that both subjects made a substantial number of responses with very brief (< 100 ms) ISIs. Of

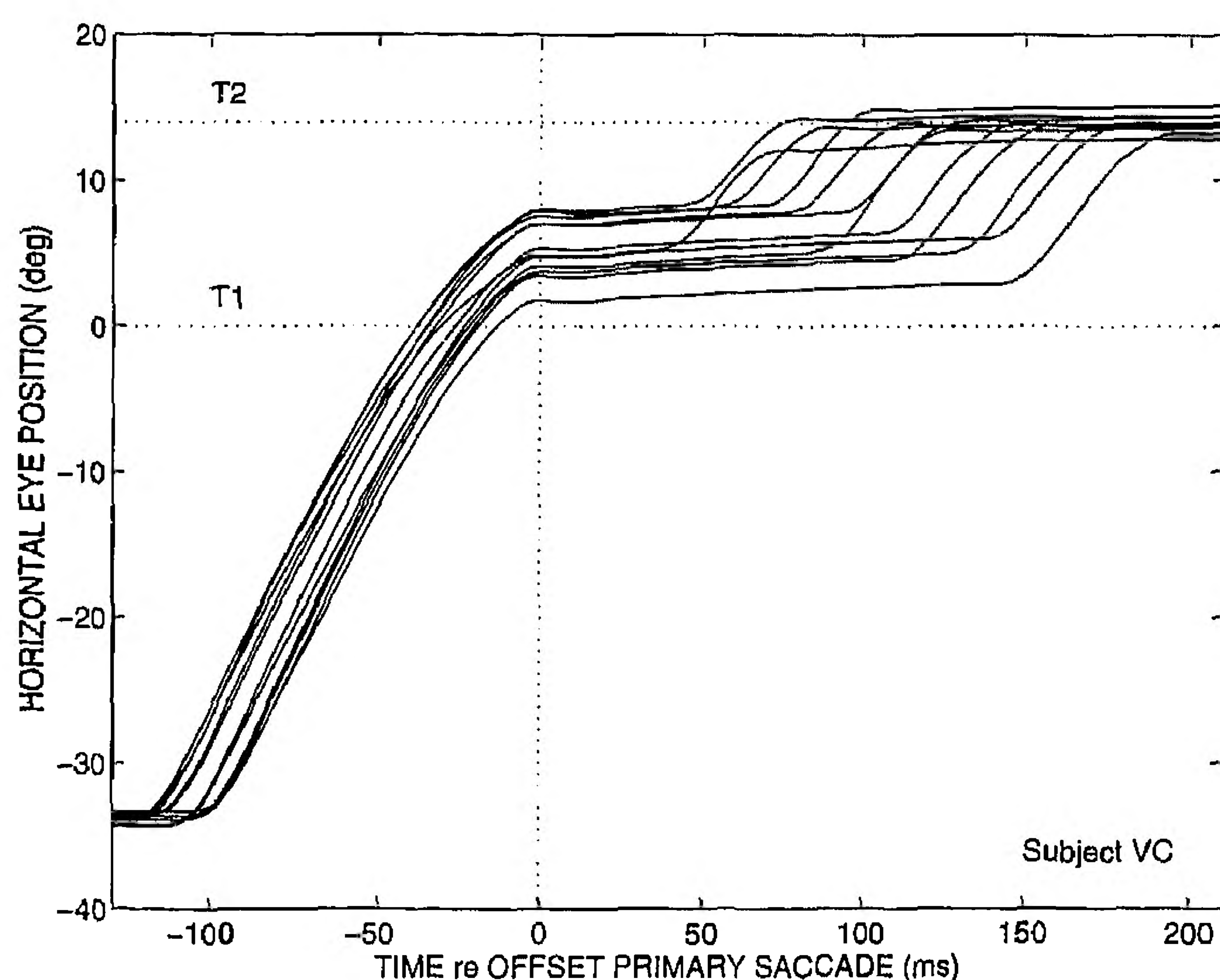


FIG. 2. Horizontal double-step responses with different intersaccadic intervals (ISIs), evoked by presentation of 2 consecutive visual targets. Data from *subject VC*. All traces are aligned with respect to offset of primary saccade. Target configuration: $F|T1|T2 = -35|0|+14^\circ$ (see METHODS). Note that despite considerable variability in large primary saccades, and despite short ISIs, all second saccades end close to 2nd target position.

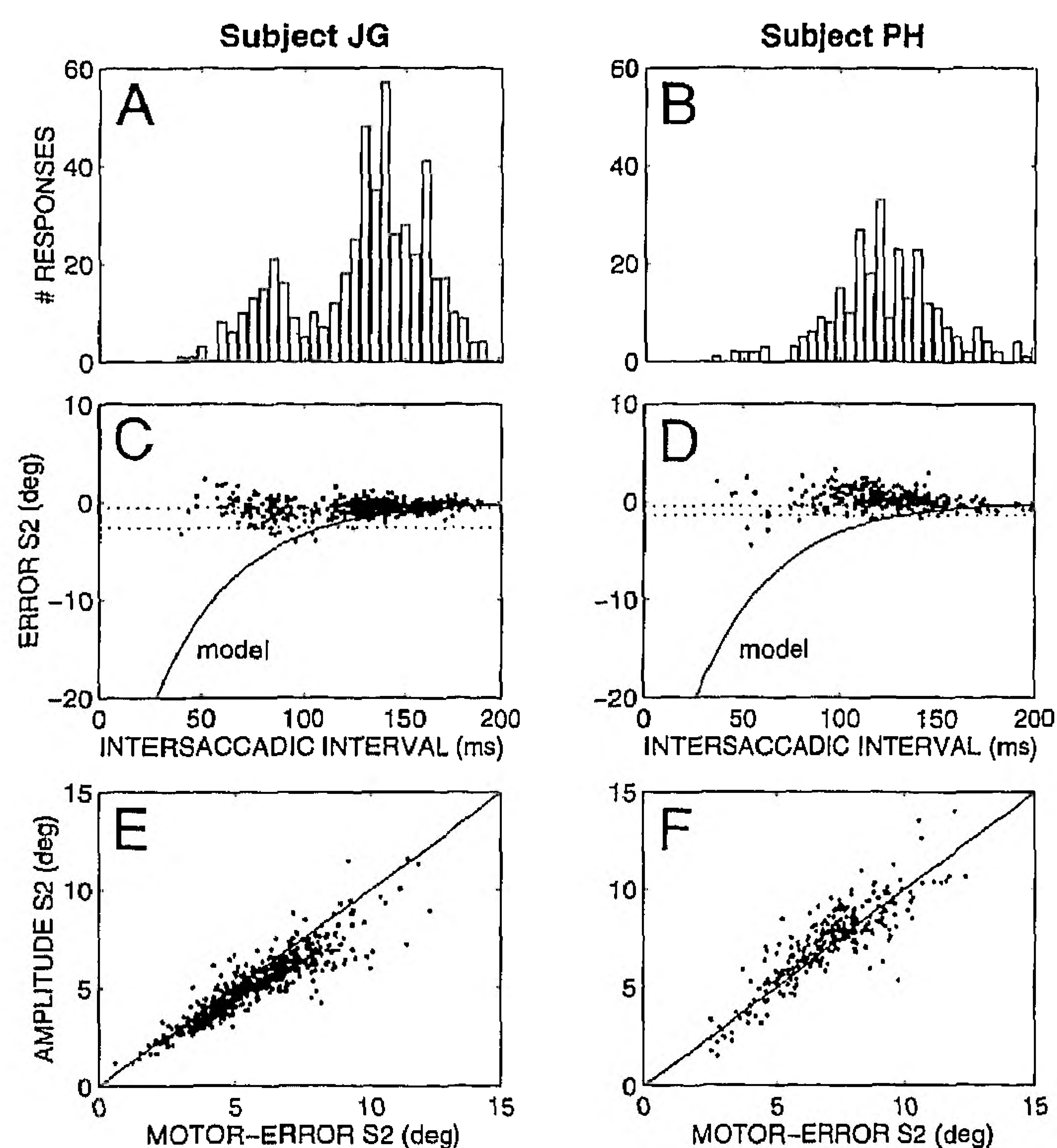


FIG. 3. Results of representative double-step experiment for 2 different subjects ($F|T1|T2 = -35|0|+9^\circ$). *A* and *B*: distribution of ISIs. Number of responses with short ISIs (< 100 ms) was $n = 104$ (20%) and $n = 47$ (17%) in *A* and *B*, respectively. Binwidth: 5 ms. *C* and *D*: horizontal error of secondary saccades (in relation to $T2$) as function of ISI. Preceding eye movements varied between 30 and 45° . Solid curve: predicted error as result of mean preceding saccade amplitude (40° in *C*; 38° in *D*), assuming an eye DI with reset time constant of $\tau = 40$ ms. Dashed horizontal lines: mean \pm SE of control saccades from $T1$ to $T2$. *E* and *F*: horizontal component amplitude of 2nd saccades vs. their initial horizontal motor error. Correlation coefficients were 0.91 and 0.87 in *E* and *F*, respectively.

all subjects, *JO* was the only subject without such short-interval responses in the double-step paradigm. For this reason, the data from *subject JO* were excluded from the model-based analysis presented below.

Figure 3, *C* and *D*, show the measured error of second saccades as a function of ISI. The solid curves (labeled "model") represent the predicted influence of the mean primary saccade according to the gradual reset hypothesis (see METHODS, Eq. 1). Note that there is a clear discrepancy between the measured errors and the predicted errors, and that the actual errors scatter around zero. The latter indicates that there are in fact no systematic errors as a function of ISI. One may observe, however, that there appeared to be a slight increase in the variability of the errors at short ISIs (see DISCUSSION).

In Fig. 3, *E* and *F*, the amplitude of second saccades is plotted versus their initial motor error. Notice the good correlation between amplitude and motor error, indicating that saccade accuracy was achieved by taking the variability in the primary saccade into account.

Figure 4, *top*, summarizes the results of each of the two double-step series (*A*: $\Delta T = 9^\circ$ and *B*: $\Delta T = 14^\circ$), by showing the pooled data of all subjects. In these plots, the difference between the measured and predicted errors (residue) is plotted as a function of ISI. So, correct predictions

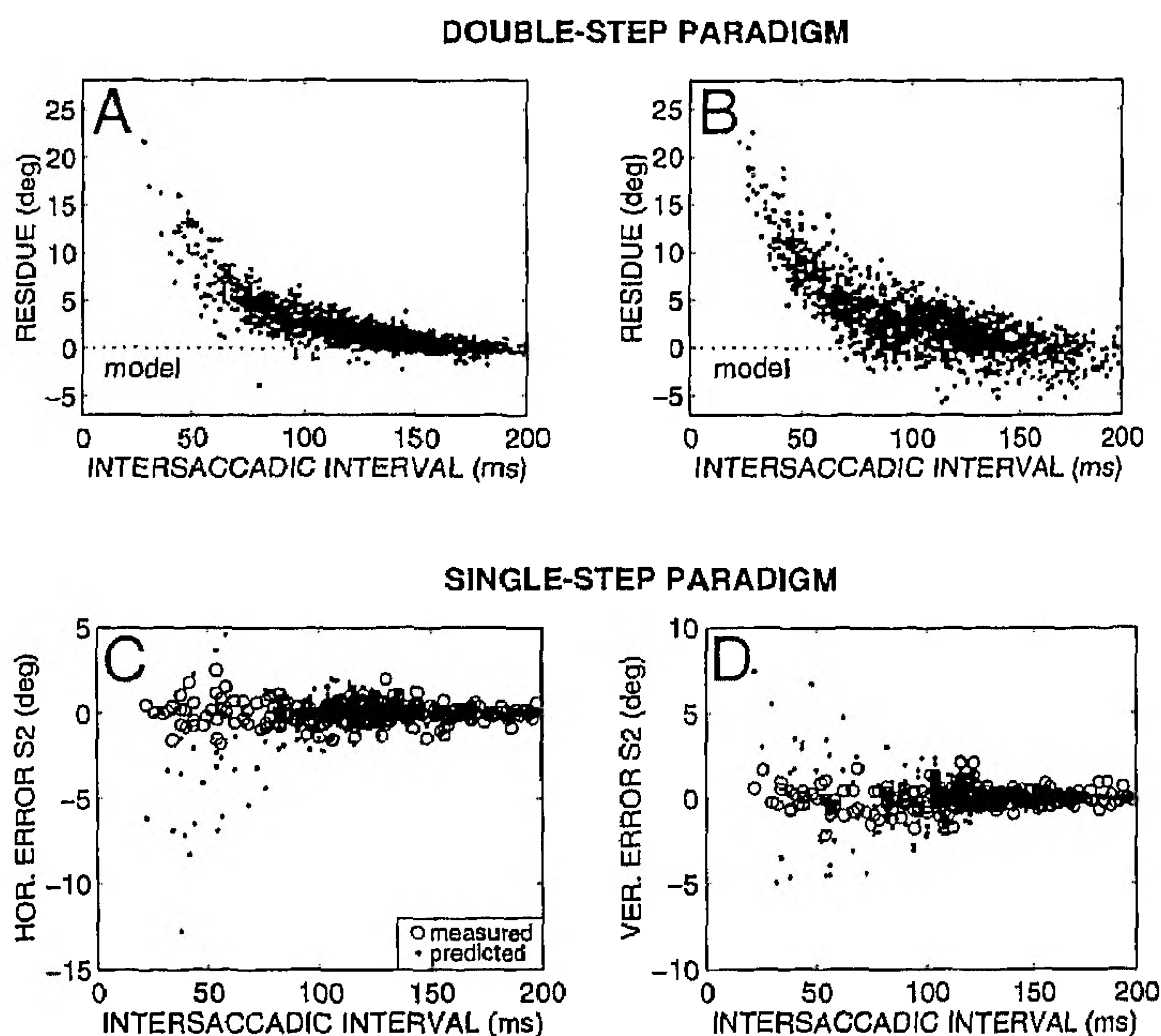


FIG. 4. *Top*: difference between actual and predicted horizontal error of 2nd saccades (residue) as function of ISI. Pooled data from all subjects, except JO. A: $\Delta T = 9^\circ$ double-step configurations ($n = 1,524$). B: $\Delta T = 14^\circ$ ($n = 1,547$). Mean residue, determined in 5-ms bins, was different from 0 (t -test, $P < 0.001$) for ISIs up to 160 and 135 ms in A and B, respectively. *Bottom*: errors of correction saccades after primary saccades to single-step visual targets. Pooled data of 4 experiments (subject JG). C: actual (○) and predicted (●) horizontal component errors as function of ISI ($0.02 \pm 0.58^\circ$, mean \pm SE, $n = 271$). D: vertical component errors ($0.03 \pm 0.61^\circ$, mean \pm SE). Measured and predicted 2-dimensional error distributions were significantly different (Kolmogorov-Smirnov test, $P < 0.001$). Error predictions were made for each individual response ($\tau = 40$ ms, Eq. 1).

of the model should fall on the horizontal dotted line (model, residue is 0). To account for the influence of the primary saccade, error predictions (Eq. 1, $\tau = 40$ ms) were made for each individual response. Notice that there is a substantial and systematic deviation between measured and predicted errors at short ISIs.

To test whether the data presented above have a more general validity, we also analyzed the corrective responses elicited by single visual targets presented at 84 random locations in the frontal plane (see METHODS). We observed that the delay between primary and corrective saccade can be very short (ISIs down to 20 ms were obtained) without affecting the accuracy of the correction saccade. This may be verified from Fig. 4, where the measured (○) horizontal (C) and vertical errors (D) of secondary eye movements are plotted versus ISI.

To show that the gradual reset hypothesis indeed predicts an influence on the saccade accuracy, the predicted errors according to Eq. 1 are also indicated (●). Note that predicted errors scatter widely for ISIs < 100 ms, and do not follow a single curve. Both features are due to the substantial variation in amplitude and direction of the primary saccades (see Eq. 1).

DISCUSSION

The results of our behavioral experiments demonstrate that the metrics of visually evoked saccades are not systemat-

ically affected by preceding eye movements, regardless of the ISI. These results corroborate earlier qualitative observations by Becker and Jürgens (1979).

Our data are equally well predicted by the position feedback model of Robinson (1975) (Fig. 1A) and more recent displacement models (Jürgens et al. 1981; Scudder 1988) (Fig. 1B), provided that the reset of the DI is close to instantaneous (estimated time constant < 10 ms). They are inconsistent, however, with the gradual reset hypothesis (Kustov and Robinson 1995; Nichols and Sparks 1995), which assumes that the putative DI is endowed with a considerable reset time constant.

Although second saccades were quite accurate, they were not entirely invariant with regard to the ISI. As may be observed in Figs. 3 and 4, C and D, the variability in the errors of second saccades was slightly larger at very short ISIs.

A possible explanation for this may lie in properties of the visual system, rather than in the premotor system. In the double-step experiments, the initial retinal error of the second target varied between 44 and 55° . This initially imposes a substantial uncertainty in target position, because of the relatively poor spatial resolution of the peripheral retina. This can affect the accuracy of second saccades if they are preprogrammed on the basis of this early visual input.

Becker and Fuchs (1969) proposed that correction saccades might be part of a preprogrammed package of two movements, because they observed that the latencies of these saccades were far less (~ 130 ms) than the primary saccades (~ 230 ms). Indeed, such a strategy may well explain why very short ISIs could be obtained in both the single- and the double-step paradigm.

Because of the predictability of saccade direction in the double-step jumps, subjects could also use a predictive strategy to generate two saccades in rapid succession. This strategy may offer an additional explanation for the slightly diminished accuracy at short ISIs. After all, a predictive response is not necessarily the correct, accurate response when there are two potential targets (see METHODS). In a few experiments it could be confirmed that prediction indeed occurred, because in catch trials the second saccade was occasionally directed in the wrong direction (i.e., away from the target; data not shown).

Note, however, that it is of no concern to the interpretation of our results whether or not the responses were predictive. Even in the case in which the saccadic system could fully preprogram the two responses, the gradual reset hypothesis would still predict the same effects as in Eq. 1.

It is important to realize that the preprogramming of an accurate second saccade would be far from trivial if the properties of a gradual resetting DI have to be accounted for as well. In that case, the saccadic system would have to 1) anticipate the ISI, 2) predict the state of the DI after the intended primary saccade, and then 3) preprogram a motor command for the second saccade that has to be substantially different from the actual required movement. In fact, even oppositely directed saccades should have to be preprogrammed under certain conditions. Although this possibility cannot be ruled out absolutely on the basis of the present behavioral data, we consider the existence of such a mechanism to be highly unlikely.

Indeed, when a complex strategy like this would be needed

to compensate for the reset properties of the DI under natural conditions (e.g., to make correction saccades), the functional significance of such an integrator in the feedback loop remains obscure. Nevertheless, such a mechanism could reconcile our data with the SC stimulation experiments. In the latter experiments, the second saccade is imposed by the experimenters, so that the saccadic system was unable to incorporate the time course of the reset.

Behavioral double-step experiments by Dassonville et al. (1992) have shown that systematic localization errors may occur when targets are flashed near the onset of a saccade. It was suggested that a sluggish, low-pass-filtered internal representation of eye position (time constant ~ 50 ms) could underlie this phenomenon. Nichols and Sparks (1995) assumed that the SC encodes the desired eye displacement (DD in Fig. 1B). In a slightly extended Robinson model, however, this collicular displacement signal and a sluggish eye position signal could be summed to obtain the desired eye position (DP in Fig. 1A). This alternative hypothesis could equally well explain the neurophysiological data (Kustov and Robinson 1995; Nichols and Sparks 1995).

Note, however, that this alternative model would also predict systematic ISI effects in our experiments. After all, immediately after the first saccade the internal representation of current eye position would be lagging the actual eye position, causing errors in the conversion of the second saccade vector into the desired eye position. As in the gradual reset model, it is not immediately obvious how preprogramming of the saccade vectors could avoid the errors introduced by the feedback dynamics.

The remarkable discrepancy between our behavioral data and the electrical stimulation data is difficult to interpret when it is assumed that postsaccadic microstimulation imposes an activity pattern in the SC that is identical to the natural behavior (Kustov and Robinson 1995; Nichols and Sparks 1995, 1996).

Interestingly, a similar discrepancy between SC stimulation data and behavioral data is observed in saccade adaptation paradigms. When the metrics of saccadic eye movements are adapted in a visual short-term adaptation paradigm, saccades subsequently evoked by microstimulation in the SC remain unadapted (FitzGibbon et al. 1986; Melis and van Gisbergen 1996). Nevertheless, during adaptation the SC activity always conforms with the desired displacement vector, although the actual saccade vector changes continuously (Frens and Van Opstal 1997). It has been suggested that the involvement of the cerebellum, which is known to be important for saccade plasticity, may be different for the two paradigms (FitzGibbon et al. 1986).

Apparently, both in the double-step paradigms (this paper; Kustov and Robinson 1995; Nichols and Sparks 1995) and in the adaptation paradigms (FitzGibbon et al. 1986; Melis and van Gisbergen 1996) there is a distinct difference between saccades elicited by visual stimuli and those evoked by microstimulation in the SC. Perhaps the spatiotemporal activation patterns in the SC induced by microstimulation are unsuitable to elicit appropriate cerebellar contributions to the brain stem saccadic burst generator.

Another possibility is that microstimulation of the SC interferes with the natural processes that determine the initiation and termination of saccades (Munoz and Wurtz 1993)

and that electrical stimulation is therefore unable to induce a timely reset of the DI.

Of course, the role of the SC is an uncertain factor in our experiments. So far, however, there is no evidence indicating that the SC is not involved in the generation of both the first and the second saccade. Moreover, we noted that the kinematics of the second saccades belonged to the same main sequence as the primary goal-directed control saccades, irrespective of the ISI, which argues against the involvement of different subsystems during first and second saccade generation. Note, however, that for the present discussion it is of no concern which subsystems may actually be involved, because they all have to converge on the final common pathway embodied by the saccadic burst generator.

We conclude that the efference copy signals involved in the feedback control of the saccadic burst generator reflect eye position and/or eye displacement accurately, irrespective of preceding eye movements.

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